ROBERTSON, OXALIDACEAE

THE OXALIDACEAE IN THE SOUTHEASTERN UNITED STATES 1

KENNETH R. ROBERTSON

OXALIDACEAE R. Brown in Tuckey, Narr. Exped. Congo 433. 1818, "Oxalideae," nom. cons. (OXALIS FAMILY)

Perennial or annual herbs [or shrubs (often dendroid), lianas, or trees].

Leaves alternate, palmately compound [or even- or odd-pinnately compound or unifoliolate], frequently in basal rosettes or apical clusters, petioled [or sessile], the petiole with a basal joint; leaflets pinnately nerved, often showing "sleep" movements, the petiolules with a basal pulvinus; stipules (or stipulelike appendages) present or absent. Inflorescences axillary or seemingly terminal [sometimes cauliflorous], bracteate, few- to many-flowered cymes, pseudoumbels [panicles or racemes] or the flowers solitary; pedicels articulated. Flowers perfect [very rarely some imperfect, the plants then androdioecious or dioecious], regular, 5merous, often heterostylous, sometimes cleistogamous; disc absent. Sepals 5, free or basally connate, persistent in fruit, imbricate in aestivation. Petals 5, free or coherent above the base, often clawed, contorted [quincuncial or cochlear] in aestivation, inserted at the base of the staminal tube. Androecium of 10 [or 15] stamens; filaments of 2 lengths, the epipetalous ones shorter than the episepalous ones, all connate below into a ring or tube, persistent in fruit; anthers dorsifixed, versatile, 2-locular at anthesis, dehiscing extrorsely by longitudinal slits. Gynoecium of 5 [rarely 3] united, superior, epipetalous carpels; styles free [or united], terminal, persistent; stigmas terminal, capitate, punctate, or penicillate, often 2-lobed; each locule with one or more anatropous, superposed, or collateral, bitegmic, tenuinucellar [or crassinucellar] ovules pendulous from an axile placenta, the micropyle apical and abaxial. Fruit a loculicidal capsule (sometimes appearing septicidal due to deep septal folds)

¹Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants in this area, with additional information from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk. The illustrations are the careful work of Karen S. Velmure. They were made from materials collected by R. J. Eaton, R. K. Godfrey, S. A. Spongberg, R. E. Umber, C. E. Wood, Jr., and myself. I am particularly grateful to Dr. Carroll E. Wood, Jr. for his continuing advice and to Dr. Alicia Lourteig, Muséum National d'Histoire Naturelle, Paris, for discussing some of her ideas on *Oxalis* with me during her recent visit to Harvard University.

224 JOURNAL OF THE ARNOLD ARBORETUM [vol. 56

[or a berry or rarely dry and indehiscent]. Seeds usually arillate; endosperm abundant [rarely absent]; embryo straight [or oblique], the radicle superior. Embryo sac development of the Polygonum type, embryo development of the Asterad type. Type GENUS: Oxalis L.

Perhaps 800 or more species in seven genera. The vast majority of species belong to Oxalis, the only genus in our area. Biophytum DC., the next largest genus (with about 70 species), is pantropical in distribution; evidently no species are common to both hemispheres. The other genera are Dapania Korth. (one species in Madagascar, two in western Malesia), Sarcotheca Blume (11 species in western Malesia), Averrhoa L. (two species, cultivated pantropically), Lepidobotrys Staudtii Engler, of tropical West Africa, and Hypseocharis Remy (nine described species of Peru, Bolivia, and Argentina). Within the family, it is clear that Oxalis and Biophytum form a natural group, while Averrhoa, Sarcotheca, and Dapania constitute another (sometimes separated as Averrhoaceae). Both Hypseocharis and Lepidobotrys are poorly known, and their affinities are less certain; they have been segregated as Hypseocharitaceae and Lepidobotryaceae. Veldkamp (1971) speculated that Hypseocharis seems to link Oxalidaceae and Geraniaceae. Hutchinson allied Averrhoaceae with the Rutales and Lepidobotryaceae (including Dapania and Sarcotheca) with the Malpighiales. There is rather general agreement (Cronquist, Hutchinson, Scholz, Takhtajan, and Thorne) that Oxalidaceae sensu stricto, Geraniaceae, Tropaeolaceae, and Balsaminaceae are related families.

Averrhoa is one of the few genera of flowering plants with more than a single species that is known only in, or as an escape from, cultivation. The geographical origin of A. Carambola L., 2n = 22, 24, and A. Bilimbi L., 2n = 22, 24, is uncertain. It is commonly said that both are of Indo-Malesian origin, since in pre-Linnaean literature they are always attributed to that region and their closest relatives are plants of Malesia and Madagascar (see Veldkamp). An American origin for the species has also been postulated, and Webster presents an example of convergent evolution in support of this hypothesis. In overall appearance Phyllanthus acidus (L.) Skeels, of the Euphorbiaceae, is remarkably similar to the two species of Averrhoa, particularly A. Bilimbi. (Linnaeus, in fact, described Phyllanthus acidus as a species of Averrhoa.) All three of these species are cultivated throughout the tropics and are of uncertain provenance. According to Webster, Phyllanthus acidus is of New World origin, since its closest congeners are from that region and since a collection from the Pará River delta in northeastern Brazil is evidently the only known specimen of this species from its native habitat. "By analogy with the documented evidence for P. acidus, it appears most likely that both species of Averrhoa are also originally American plants which have had a similar history. The great superficial resemblance between these three species may not be entirely coincidence, for it is possible that all three are members of the sub-littoral forests of the South American coastline; and their similarity in life form

1975] ROBERTSON, OXALIDACEAE

may have a selective basis. Probably, as suggested by Merrill and Trimen, these plants were first encountered by the Portuguese on the Brazilian coast and from there carried to India and other parts of the Old World" (Webster).

225

Heterostyly is common in the family. Many species of Oxalis, a few of Biophytum, and Averrhoa Bilimbi are tristylous. Distyly occurs in Averrhoa Carambola and in species of Oxalis, Biophytum, Sarcotheca, and Dapania (with two species androdioecious). Some species of Oxalis and Biophytum are homostylous. The species of Hypseocharis evidently are homostylous, although the styles elongate after anthesis. Lepidobotrys Staudtii is described as dioecious. Cleistogamous, as well as chasmogamous, flowers occur in certain maximum of Ourline

flowers occur in certain species of Oxalis.

It has been postulated that the breeding system of ancestral Oxalidaceae combined morphological heterotristyly and physiological self-incompatibility (see Ornduff; Eiten argues, however, that homostyly is the original condition). In the idealized oxalidaceous tristylous system, there are three positions or levels for the one set of stigmas and the two sets of anthers. Long-styled flowers have the stigmas at the highest position, with the two sets of anthers at the middle and lowest positions. In midstyled flowers, one set of anthers is in the highest position, the stigmas are in the center position, and the other set of anthers is in the lowest position. The anthers occupy the upper and center positions in the short-styled flowers, with the stigmas in the lowest position (see FIGURE 1, o-q). In addition to differing in the lengths of the styles and filaments, the three types of flowers can differ in the size of the pollen grains (which are largest in anthers of the upper level and smallest in anthers of the lowest position), in the shape of the stigmas, in the pubescence of the filaments and styles, and in the curvature of the styles. In this idealized situation, pollen from anthers of the uppermost position of midstyled and shortstyled flowers will be compatible only with stigmas of long-styled flowers; pollen from anthers of the middle level of long- and short-styled flowers will germinate only on stigmas of midstyled flowers; and pollen of the lowest position of long-styled and midstyled flowers will be compatible only with stigmas of short-styled flowers. Some species, among them Oxalis valdiviensis Barnéoud (Chile), O. Regnellii Miq. (South America), and O. purpurea L. (including O. speciosa Ecklon & Zeyher; South Africa), have retained this type of breeding system of tristyly and self-incompatibility. However, it seems that many or most species of the family have shifted away from a system that requires cross-pollination toward ones that allow autogamy. In many cases, there is a partial to complete loss of self-incompatibility, which may or may not be accompanied by morphological changes. Thus, some populations of O. Dillenii subsp. filipes are strongly tristylous and wholly selfcompatible. According to Denton (p. 482), the reverse occurs in Oxalis sect. IONOXALIS, and even the homostylous species are self-incompatible. One or two of the possible flower forms may be lost within a species, resulting in distyly or homostyly. Only long- and short-styled flowers

seem to occur in Oxalis violacea, O. Priceae subsp. Priceae, Biophytum Petersianum Klotzsch., Dapania pentandra, and the species of Sarcotheca. Long-styled and midstyled flowers are found in O. albicans and Averrhoa Carambola. Evidently, only long-styled flowers occur in O. thelyoxys (Cuba), O. magellanica (Southern Hemisphere), and O. Acetosella subsp. Griffithii (Asia). It is sometimes said that this is the situation in O. Acetosella subsp. Acetosella and subsp. montana, but an examination of herbarium specimens shows that the level of insertion of the stigmas is mostly either considerably above the upper whorl of anthers or slightly below them; it needs to be determined whether this is a variable character or a case of distyly with long-styled and midstyled flowers. Darwin thought that European populations were variable in this respect. The distance between the stigmas and anthers is small enough in some species, or in populations of some species, to ensure self-pollination, even though the flowers are heterostylous. Ornduff (1972) called such flowers "quasi-homostylous" and noted their occurrence in Oxalis Dillenii subsp. filipes and subsp. Dillenii. Another mechanism that promotes self-pollination is a change in the relative lengths of the filaments and styles so that the stigmas are inserted at the same level as either the upper or lower whorl of anthers. This condition, termed "semihomostyly," has been observed in O. Dillenii subsp. filipes and subsp. Dillenii, and in a species of Biophytum (Mayura Devi, 1966).²

226

According to Veldkamp (1971), the pollen is shed in the buds of some species of Biophytum. Evidently, some seemingly normal flower buds of certain Oxalis species do not open, but are autogamous and set fruit; this seems to occur mostly late in the growing season, at least in Massachusetts. Much reduced, truly cleistogamous flowers are produced in O. Acetosella and some other species (see FIGURE 1, c). Several different genetic systems have been proposed to explain the inheritance of style length in the few species of Oxalis that have been studied in this respect (see discussion and table in Mulcahy). Two species that occur in our area, O. Priceae and O. Dillenii subsp. filipes (see Mulcahy and Ornduff, respectively), seem to have a system with two loci and two alleles at each locus. "Short" is dominant and has the generalized genotype of S___mm or S___M___. "Medium" is recessive to "Short" and its genotypes are ssMm or ssMM. "Long" is a double recessive, ssmm. Although much has been written about breeding systems of Oxalis, very few species have been examined in detail, and it may very well be that generalizations accepted now will have to be changed.

The family is of only slight economic importance. Several species of Oxalis are cultivated as ornamentals; some are especially well suited to the rock garden and alpine house. Averrhoa Carambola is cultivated commercially to some extent and in dooryards in southern Florida. The yellow to orange, deeply angled fruits, star-shaped in cross section and up

² Mayura Devi identifies the plants as Biophytum sensitivum DC., but Veldkamp (1971) says they certainly do not belong to this species.

ROBERTSON, OXALIDACEAE

to five inches long, vary greatly in degree of acidity from tree to tree. The fruits are eaten fresh, used in drinks, or made into jelly and jam. The flavor and odor are sometimes likened to quince, Cydonia oblonga. Averrhoa Bilimbi, the cucumber or pickle tree, which has rather cylindrical, extremely acid fruits that are used in drinks, jellies, pickles, and curries, is seldom grown in Florida. Leaves of Oxalis species are used in salads, but excess use should be avoided because of the presence of oxalic acid. Oxalis Pes-caprae and O. corniculata are known to accumulate lethal concentrations of soluble oxalates under certain conditions. Oxalis tuberosa Molina, oca, 2n = 14, 60, 63-64, 68-70, is a major food crop in Andean South America, particularly in the area around Lake Titicaca. The tubers contain large amounts of oxalates and are treated in various ways, such as by submerging them in water for several weeks and then placing them in open areas, where they are exposed to freezing by night and drying by day. Several species of Oxalis sect. CORNICULATAE act as aecial hosts for the maize, sorghum, and andropogon rusts (see discussion in Eiten, 1963).

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228 JOURNAL OF THE ARNOLD ARBORETUM [vol. 56

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1. Oxalis Linnaeus, Sp. Pl. 1: 433. 1753; Gen. Pl. ed. 5. 198. 1754.

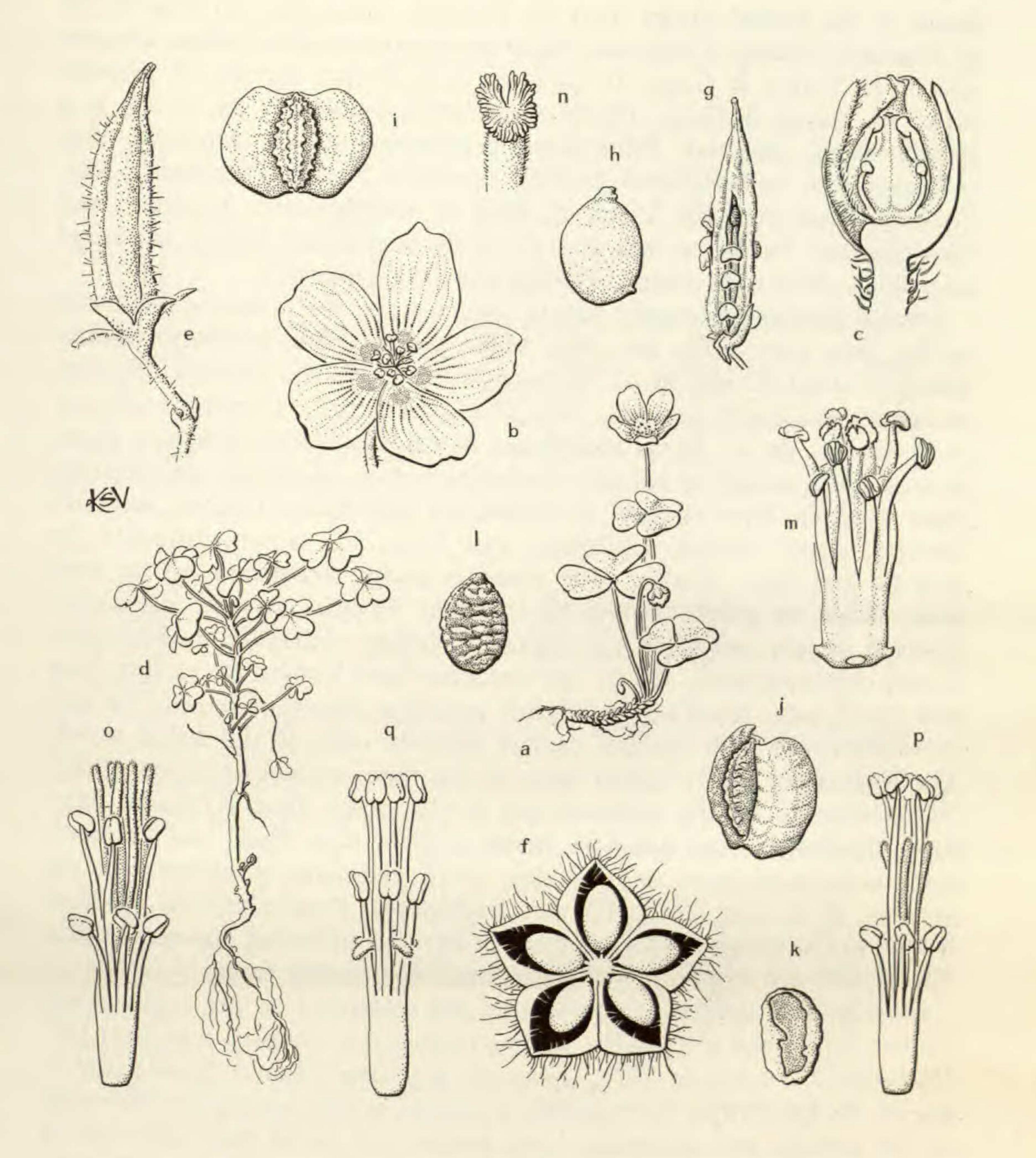
Perennial or annual, caulescent or acaulescent herbs [rarely undershrubs], sometimes with bulbs (often with contractile roots below) or rhizomes [or tubers]. Indumentum of septate and/or nonseptate trichomes that vary in length, shape, density, and distribution. White or sometimes orange, red, or black calcium oxalate deposits frequent on sepal apices, bracts, bulb scales, and leaves, infrequent on petal tips and gynoecia. Leaves basal and/or cauline (often in apical clusters), trifoliolate [to many-foliolate or rarely unifoliolate], often heteroblastic, long petiolate [to nearly sessile], the petiole with a persistent, basal articulation; leaflets often with reddish or purple markings, mostly obcordate or emarginate [or entire or deeply divided], nearly sessile, with a basal pulvinus, folding and drooping at night; stipules absent or small, paired, and adnate to the basal articulation of the petiole. Inflorescences from basal rosettes or axillary, the flowers solitary or in few- to manyflowered cymes or modified cymes, such as pseudoumbels. Flowers tristylous, distylous, homostylous, semihomostylous, or quasihomostylous. Petals shortly clawed below, yellow, orange, white, or violet [to red], the base of the blade often with nectar guides, withering after expansion, sometimes forming a calyptra on the fruit. Filaments monadelphous below, alternate ones longer and sometimes with an abaxial appendage. Carpels 5, connate adaxially, free laterally; styles free, erect in longand midstyled flowers, abaxially curved and projecting between the filaments in short-styled flowers; stigmas punctate, capitate, or penicillate, faintly to prominently 2-lobed. Capsules globose, oblate, or broadly to narrowly cylindric, often 5-angled or star-shaped in cross section, dehiscing by loculicidal slits (often appearing septicidal), the valves persistent. Seeds in the capsule each enclosed by a turgid, translucent aril that turns inside out explosively; seed flattened, elliptic with pointed ends, often with transverse and/or longitudinal ridges; endosperm present [or absent]. (Including Acetosella Kuntze, 1891, not Fourreau, 1869; Bolboxalis Small; Ionoxalis Small; and Xanthoxalis Small.) TYPE SPECIES: O. Acetosella L.;

JOURNAL OF THE ARNOLD ARBORETUM [VOL. 56 230

see J. K. Small, N. Am. Fl. 25(1): 25. 1907. (Name from Greek, oxys, acid, in reference to the supposed medicinal use of these plants; see Linnaeus, Phil. Bot. ed. 1. 184. 1751. This name was used by the ancient Greeks for Rumex Acetosella and was first applied to this genus by Linnaeus.) --- WOOD-SORREL.

Estimates of the number of species range from 300 to more than 800, the latter probably being closer to the actual number. The genus is cosmopolitan but is most diverse in South Africa and South America, and, to a lesser degree, in Central America and Mexico; relatively few species are indigenous to North America and Eurasia. In the world-wide treatment of the family for Das Pflanzenreich, Knuth recognized 791 species of Oxalis, grouping them primarily on variations in stem structure into 37 mostly unnatural sections and numerous subsections and series. Since that time, important taxonomic treatments include Salter's study of the genus in South Africa, Eiten's synopsis of sect. CORNICULATAE, and Denton's monograph of the North American species of sect. IONOXALIS. Currently, Dr. Alicia Lourteig is in the midst of a major world-wide revision of the genus (exclusive of the South African species) with particular emphasis on the poorly understood South American species. Small (Fl. Southeast. U. S. 1903; N. Am. Fl. 1907) placed the North American species of Oxalis in eight genera. His scheme has not been adopted generally, and, in view of the variation that occurs within Oxalis on a world-wide basis, it seems best to recognize only one inclusive genus. Section OXALIS (sect. Acetosellae Knuth) (flowers solitary from elongated, underground rhizomes) is represented in our area by Oxalis Acetosella subsp. montana (Raf.) Hultén ex D. Löve (O. montana Raf.), 2n = 22, which occurs in rich, moist woods from Newfoundland and eastern Quebec to Manitoba and Saskatchewan, south to Pennsylvania, eastern Ohio, Kentucky, Michigan, Wisconsin, and Minnesota, and in the mountains of the Virginias, North Carolina, and Georgia. The attractive flowers of this plant have white or light pink petals marked with darker pink veins and basal yellow spots. Individuals with solid dark pink or purplish flowers can be referred to f. rhodantha Fern. In the chasmogamous flowers of this subspecies, the stigmas are either considerably above the upper whorl of anthers or slightly below them (see family discussion). Reduced, cleistogamous flowers are also produced, particularly late in the growing season. Young (1968) notes that the cleistogamous flowers of the European populations are apetalous, but at least some of the cleistogamous flowers on North American plants have small petals (see FIGURE 1, c). Oxalis Acetosella has a very broad distribution (see maps in Veldkamp, 1971, and Hultén). Subspecies Acetosella is Eurasian, occurring from Iceland, the British Isles, and Scandinavia, south to Spain, Italy, and Anatolia, and west to the Caucasus Mountains, China, Korea, Kamchatka, and Japan. Subspecies Griffithii (Edgew. & Hooker f.) Hara, 2n = 22, is mostly of southern and western Asia, from northwestern India through China to Japan, Formosa, and the Philippine Islands. Related plants are

ROBERTSON, OXALIDACEAE



231

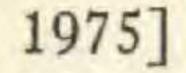
FIGURE 1. Oxalis sections Oxalis (a-c) and Corniculatae (d-q). a-c, O. Acetosella subsp. montana: a, plant with chasmogamous flower and immature fruit from cleistogamous flower — note persistent swollen leaf bases on rhizome, \times ¹/₂; b, chasmogamous flower, veins of petals deep pink, basal spot yellow, \times 2; c, cleistogamous flower in off-center vertical section, upper set of anthers touching stigmas, lower set of anthers sterile, \times 12. d-l, O. stricta: d, habit, \times ¹/₂; e, mature fruit before dehiscence, \times 3; f, same in cross section, carpels free laterally, seeds enclosed by aril, dehiscence through loculicidal slits, \times 12; g, capsule during dehiscence — note seeds and arils, \times 3; h, seed enclosed by aril, \times 12; i, j, two views of aril splitting away from seed, \times 12; k, aril after eversion, \times 12; l, seed, \times 12. m, n, O. Dillenii subsp. filipes: m, androecium and gynoecium from quasi-homostylous flower, \times 10; n, penicillate, 2-lobed stigma, \times 25. o-q, O. grandis: androecium and gynoecium from long-styled, midstyled, and short-styled flowers, respectively, semidiagrammatic, \times 6.

JOURNAL OF THE ARNOLD ARBORETUM [vol. 56

found in the United States from the Olympic Mountains of Washington to Monterey County, California; these are treated as either subsp. oregana (Nutt. ex Torrey & Gray) D. Löve or as a distinct species, O. oregana Nutt. ex Torrey & Gray. Oxalis magellanica Forster f., 2n = 10, is a closely allied, Southern Hemisphere counterpart of O. Acetosella that is known from Andean South America (southern Peru to Patagonia), New Zealand, Tasmania, the Victorian Alps of southwestern Australia, and New Guinea. Veldkamp indicates that only long-styled flowers are found in both O. Acetosella subsp. Grifithii and O. magellanica.

232

Section IONOXALIS (Small) Knuth (acaulescent, the flowering peduncles arising from scaly bulbs, the petals violet, purple, pink, or white) is composed of about 50 species of the New World, with the greatest diversity in Mexico and South America. Only Oxalis violacea L. (Ionoxalis violacea (L.) Small), 2n = 28, is indigenous in eastern North America, where it occurs in a variety of habitats, including woods, pinelands, and prairies, from southern New England to Minnesota and South Dakota, south to Georgia, upper Florida, Louisiana, and Texas. It occurs disjunctly in Arizona and New Mexico. The plant is easily recognized by its dark pink, violet, or purple (white in f. albida Fassett) flowers in severalflowered, simple umbels on unbranched peduncles that overtop the leaves, by the oblate capsules, and by the moderate-sized leaflets (8-15 mm. long and 10-23 mm. broad) with reddish markings above or a solid reddish cast below and with calcium oxalate deposits only at the apical notch. The leaflets are partly folded most of the time, seldom expanding fully. The plants are usually glabrous, but in the region from Arkansas, Missouri, Mississippi, and Alabama, north to Ohio, New York, and Vermont, some individuals have multicellular, often glandular, trichomes on the petioles; these may be called var. trichophora Fassett. Oxalis violacea flowers in the spring and often again in late fall following autumnal rains. The flowers are distylous with long- and short-styled forms. Several other species of this section are cultivated in the southeastern United States, and a few have become established. Oxalis corymbosa DC. (including O. martiana Zucc., Ionoxalis martiana (Zucc.) Small), 2n = 24, 28, 30, has flowers in irregularly branched cymes, nonseptate trichomes on the petioles and peduncles, large leaflets (27 to 46 mm. long and 34 to 63 mm. wide) that are mostly fully expanded during the day, randomly distributed calcium oxalate deposits in the leaflets, and usually abundant bulblets. A native of South America, it is found in scattered localities from South Carolina to Florida and Texas; it is also widespread in the West Indies. According to Denton, this species does not set seed in North America (although Small describes capsules and seeds), and Veldkamp (1971) reports the same situation in Malesia. Small recorded O. intermedia A. Rich. (as Ionoxalis intermedia (A. Rich.) Small) from hammocks in southern peninsular Florida, and Denton noted a variant allied to this species from Sarasota, Florida. Oxalis intermedia is readily recognized by its obdeltoid leaflets. Evidently escaped from cultivation in the Carolinas and perhaps else-



ROBERTSON, OXALIDACEAE

233

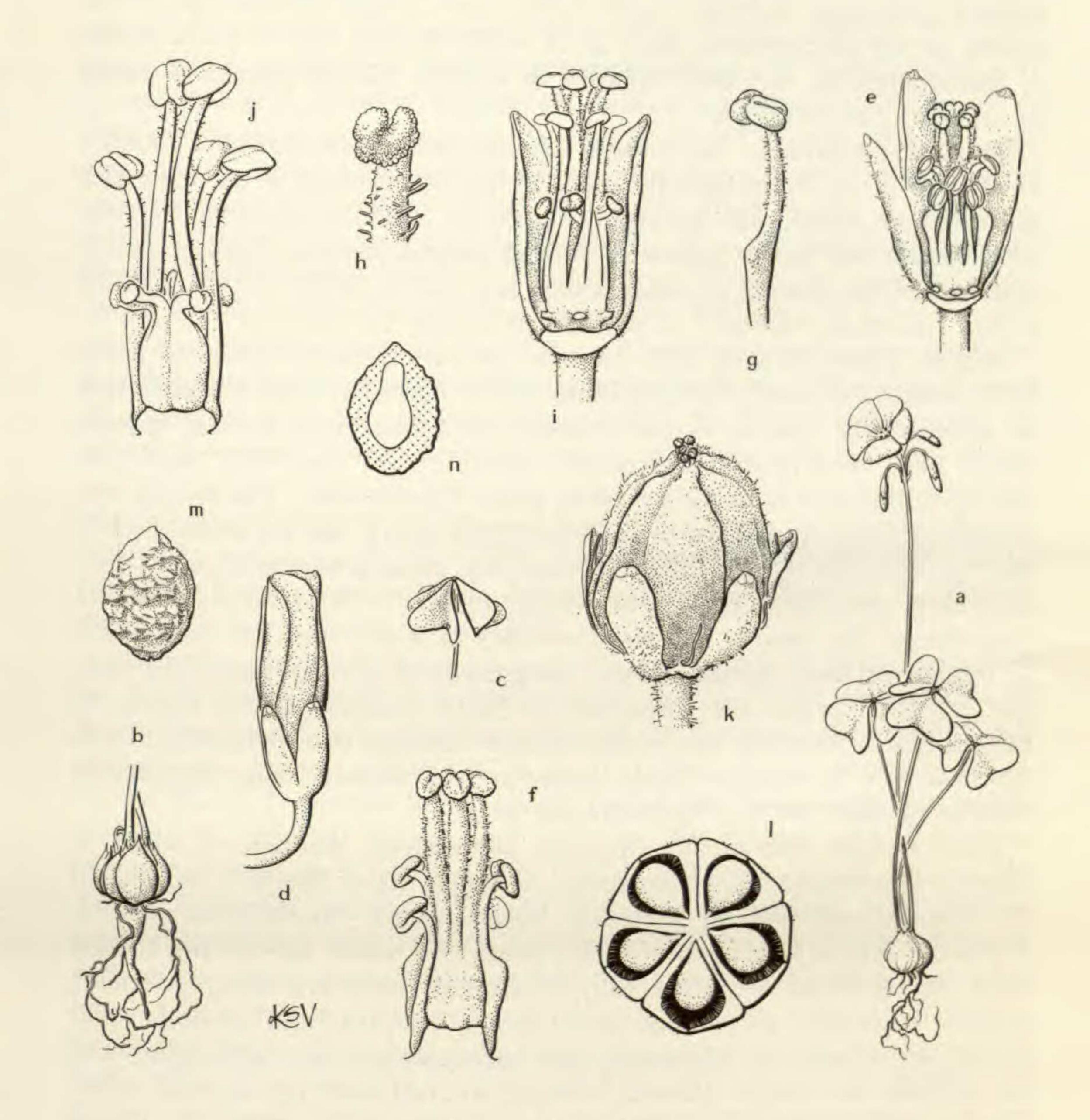


FIGURE 2. Oxalis section Ionoxalis. a-n, O. violacea: a, flowering plant, $\times \frac{1}{2}$; b, scaly bulb with contractile taproot below, $\times 1$; c, leaflets in folded position — note oxalate deposits at apex of notch, $\times \frac{1}{2}$; d, flower bud, petals contorted, $\times 3$; e, long-styled flower, petals (scars indicated by open circles) and 2 sepals removed — note abaxial appendages on longer filaments, $\times 6$; f, androecium (4 stamens removed) and gynoecium from long-styled flower, $\times 10$; g, longer stamen from long-styled flower, $\times 12$; h, tip of style and stigma from longstyled flower, $\times 25$; i, short-styled flower, petals and 2 sepals removed, $\times 6$; j, androecium and gynoecium from short-styled flower, $\times 10$; k, nearly mature capsule from short-styled flower, $\times 5$; l, same in cross section, placentation axile, dehiscence through loculicidal slit, carpels connate only adaxially, seeds enclosed by aril, $\times 6$; m, seed with aril removed, $\times 12$; n, seed in vertical section, endosperm even-stippled, embryo unshaded, $\times 12$.

JOURNAL OF THE ARNOLD ARBORETUM VOL. 56 234

where are plants superficially rather similar to O. corymbosa, but which have fleshy, more or less cylindrical rootstocks (not scaly bulbs) and densely pubescent pedicels, calyx lobes, and petals. These plants are known in the horticultural trade as O. rubra St.-Hil., 2n = 42, a native of South America, but their identity is suspect. Knuth placed O. rubra in his sect. ARTICULATAE.

Oxalis Pes-caprae L. (O. cernua Thunb., Bolboxalis cernua (Thunb.) Small), 2n = 28, indigenous to South Africa, is cultivated in our area and, according to Small, has perhaps escaped at least in northern Florida. This species has showy yellow flowers in several-flowered, leafless cymes that exceed the rosette of basal leaves and has a caudex at the apex of a long contractile taproot. It reproduces mostly by bulbils. Section CORNICULATAE DC. (flowers yellow, stems creeping to erect, bulbs absent) is mostly of temperate North America. The nomenclature of some of the species is particularly confusing, since several specific names have been applied differently. Small placed the North American species of this section in his segregate genus Xanthoxalis. The section was revised by Eiten (published in an abbreviated form), and his nomenclature and classification, which differ substantially from previous accounts, are used here, since both have been widely adopted. Dr. Lourteig's studies may change the number of taxa, the ranks at which they are recognized, and some of their names. Eiten recognized 14 species and eight subspecies; five species are restricted to South America, three mostly to eastern North America, two to the Greater Antilles, two to western North America, one to eastern North America and eastern Asia (introduced elsewhere), and one is a cosmopolitan weed. Eiten divided this section into two subsections, the first of which is subsect. CORNICULATAE. (According to Article 22 of the 1972 edition of the International Code of Botanical Nomenclature, this becomes subsect. BOREALES Knuth.) In species of this group, the stems are usually several from the crown of a taproot (any horizontal stems are above ground); septate trichomes are absent from stems, petioles, and pedicels (but sometimes present on capsules); the inflorescences are umbellate; and the pedicels are usually strongly reflexed in fruit with the capsules erect. Oxalis corniculata L. (Xanthoxalis corniculata (L.) Small, O. repens Thunb., X. Langloisii Small), 2n = 24, 36 (38?), 42, ca. 46, 48, is a pantropical weed with creeping stems rooting at the nodes, broadly auriculate stipules, and small, mostly homostylous flowers. This species, evidently native to the Old World and extremely variable in Australasia, is a troublesome lawn weed in warm regions and is frequently encountered as a weed in greenhouses farther north. Several varieties have been described, but Eiten recognized only one polymorphic species. Another group of plants of this subsection, with erect flowering stems that do not root at the nodes, is taxonomically and nomenclaturally difficult. Eiten grouped them into two species and five subspecies. Plants with small, mostly homostylous flowers (petals less than 13 mm. long)

1975] ROBERTSON, OXALIDACEAE 235

belong to Oxalis Dillenii Jacquin, while those with larger strongly tristylous flowers (petals mostly longer than 15 mm.) belong to O. Priceae Small. Two subspecies of O. Dillenii based on differences in the indumentum of the capsules were recognized by Eiten: subsp. Dillenii (O. stricta auct., not L. [following Eiten's lectotypification], O. florida Salisb., O. Lyonii Pursh, O. Navieri Jordan, O. recurva var. floridana Wiegand, O. Dillenii var. radicans Shinners), 2n = 18, 20, 22, 20-24, which is common nearly throughout eastern North America (locally naturalized in Europe) and subsp. filipes (Small) Eiten (O. filipes Small, O. Brittoniae Small, O. florida var. strigosifolia Wiegand), 2n = 16, which occurs from Florida to Louisiana, north to Connecticut, Tennessee, and Missouri. Oxalis Priceae (O. recurva Elliott, nom. dub. according to Eiten) is confined to the southeastern United States; Eiten recognized three subspecies that differ in the pubescence of the stems and pedicels. Subspecies Priceae (O. cespitosa Raf., not O. caespitosa St.-Hil., O. hirsuticaulis Small) occurs in Kentucky, Tennessee, Mississippi, Alabama, and Georgia; subsp. colorea (Small) Eiten (Xanthoxalis colorea Small) occurs along the coast from North Carolina to Florida and Louisiana; and subsp. texana (Small) Eiten (X. texana Small, O. recurva var. texana (Small) Wiegand) occurs in eastern Texas and Louisiana and in scattered localities on the Coastal Plain to northern Florida and Georgia. Subsection STRICTAE Eiten of sect. CORNICULATAE is characterized by the stems arising singly from underground rhizomes; the presence of septate trichomes on stems, petioles, and pedicels; cymose inflorescences; and pedicels that are not reflexed in fruit. It includes Oxalis stricta L., 2n =18, 24, 18-24, O. grandis Small, and O. Suksdorfii Trelease, the last mostly confined to western Oregon and adjacent Washington and California. Plants from eastern North America (Newfoundland to North Dakota and British Columbia, south to Florida, Arkansas, Oklahoma, New Mexico, and Arizona) and from eastern Asia (extensively naturalized in Europe) with small, mostly homostylous flowers (the petals usually less than 1 cm. long) and with leaves lacking colored margins were called O. stricta L. by Eiten. These plants have had a tortuous nomenclatural history, having been called O. corniculata by Gray, Xanthoxalis cymosa, X. Bushii, and X. rufa by Small, and O. europaea by authors of numerous twentieth-century manuals and floras; the eastern Asiatic plants are usually known as O. fontana Bunge. The name "Oxalis stricta L." was first lectotypified by Robinson and was applied by him to those plants Eiten called O. Dillenii. Eiten rejected Robinson's typification and used the name for the plants native to eastern North America and eastern Asia. Dr. Lourteig has indicated in conversation that she thinks Robinson's typification is correct, that the name O. stricta should be applied to those plants Eiten called O. Dillenii, and that O. fontana is the correct name for the plants Eiten called O. stricta. Oxalis grandis Small is a very attractive species with large, red- or purple-margined leaflets and showy, strongly tristylous flowers. These

plants occur in rich woods, usually in the mountains, rarely on the Upper Piedmont, from Pennsylvania to southern Illinois, south to Georgia, Alabama, Tennessee, and Kentucky.

The carpels of many species of Oxalis are connate only toward the floral axis, with most of the lateral walls being free and merely closely juxtapositioned (see FIGURES 1, f, and 2, 1). To the casual observer, it appears that the capsules are septicidal because of the folds (the "episeptal rimae" of Veldkamp) between the carpels. However, dehiscence takes place through a loculicidal slit on the abaxial side of each carpel. At maturity, the slits open slightly, and the abaxial carpel walls are thin and flaplike. The seeds are enclosed by a smooth, turgid aril, which splits suddenly along an abaxial suture and turns inside out. This motion ejects the seed, and often the aril, through the slit to a considerable distance from the parent plant. The ejection of one seed sets off a chain reaction that results in the dispersal of most seeds in one capsule in a very short time. The seeds of some species, such as O. corniculata, are sticky and adhere to objects on which they land.

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236

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